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EVOLUTIONARY MODIFICATIONS OF ONTOGENY OF THREE *DECHENELLA* SPECIES (PROETIDAE), FROM THE MIDDLE DEVONIAN OF THE ARDENNE MASSIF (FRANCE)

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ABSTRACT—Numerous exuviae of three *Dechenella* species (*D. givetensis*, *D. ziegleri* and *D. calxensis*) from the Middle Devonian (Givetian) of NE France (Ardenne Massif) provide the opportunity to identify the evolutionary modifications of ontogeny of the three *Dechenella* species and to elaborate a conceptual framework of developmental shape changes. First we used biometric and morphometric approaches to characterize shape modifications. Then we computed ontogenetic trajectories by multivariate regression of geometric shape variables on centroid size in order to compare them. Finally, we compared parallelism between trajectories and rates of development relative to size. These analyses demonstrate a significant difference in the cranidial developmental trajectories of *D. givetensis* and *D. ziegleri* indicating an allometric repatterning. However, pygidia of these species share the same allometric pattern with a distinct developmental rate suggesting that heterochrony could be a partial explanation for the body shape evolution. Pygidial ontogeny of *D. calxensis* corresponds to an allometric repatterning with respect to both other species. This work illustrates the complexity of evolutionary modifications of ontogeny constituting an important process in morphological novelties.

INTRODUCTION

DEVELOPMENTAL MODIFICATIONS are a major causal factor in morphological disparity. During the last few decades, developmental modifications have been mostly investigated under the heterochrony notion (Gould, 1977; Alberch et al., 1979; McNamara, 1986). Nevertheless, evolutionary changes in ontogeny are not limited to modifications of developmental rate or timing corresponding to heterochronies (e.g., Alberch, 1985; Gould, 2000). Evaluating heterochrony in fossil taxa has not been helped by excessive terminology (e.g., Klingenberg, 1998; McKinney, 1999). To clarify the problem, Webster and Zelditch (2005) proposed only six modes of evolutionary changes of ontogeny and gave methodological procedures using geometric morphometrics to identify them. The development of these multivariate shape analyses has allowed a better quantification of the modifications occurring during ontogeny (e.g., Webster et al., 2001; McNamara, 2002; Hunda and Hughes, 2007; Gerber et al., 2007).

In the present paper, the developmental modifications of three Givetian species belonging to the genus *Dechenella* Kayser, 1880 (Proetidae) were examined: *D. givetensis* Bignon and Crônier, 2011, *D. ziegleri* Struve, 1992 and *D. calxensis* Bignon and Crônier, 2011. The studied material comes from the Mont d'Haurs section, in Givet, northeast France. With over 50 named species *Dechenella* is among the most diverse genera of Middle Devonian trilobites. Ontogenetic comparisons can aid in determining which of these species are valid. Descriptions of ontogenetic development were obtained for other Devonian proetids subfamilies by Chatterton (1971), Lerosey-Aubril and Feist (2005, 2006), Feist and Lerosey-Aubril (2005) and Lerosey-Aubril (2006). Unfortunately, the development of *Dechenella* is still sporadically described (Selwood, 1965; Chlupáč, 1992; Chatterton et al., 1999).

Trilobites bear on their exoskeleton an important number of biological structures suitable for geometric morphometric analyses based on landmarks. Such studies were successfully performed on the trilobites to describe ontogenetic shape changes and to discriminate taxa (e.g., Hughes and Chapman, 1995; Webster et al., 2001; Kim et al., 2002; Crônier et al., 1998, 2004, 2005; Webster and Zelditch, 2005; Hunda and Hughes, 2007; Webster, 2007; Delabroye and Crônier, 2008).

Thereby, a landmark-based analysis was applied on the cranidial and pygidial features of three *Dechenella* species in order 1) to quantitatively discriminate species; 2) to identify patterns of shape and size modification during the ontogeny; and 3) to determine the modes of evolutionary changes of ontogeny.

METHODS

Biometric analysis: dimensions and size distribution.—We performed a hierarchical classification based on width and length linear dimensions on each species in order to establish size classes and to assign each specimen to a particular ontogenetic phase. Without biological evidence to differentiate ontogenetic instars, we considered the most inclusive groups defined by the cluster analyses: three for the cranidia and four for the pygidia (Fig. 1). A single specimen represents *D. ziegleri* for the ontogenetic phases 3 (cephalon) and 4 (pygidium). As for *D. calxensis*, the cephala are unknown and few pygidia are available for this analysis. Consequently, only two size classes were determined for *D. calxensis* to approach the mean centroid size of the ontogenetic pygidial phases of both other species as well as possible. Univariate Analyses of Variance (ANOVAs) indicated a significant size differentiation among these ontogenetic phases (Table 1). In this paper, the term ''ontogenetic phase'' is favored over ''ontogenetic stage'' because there is no biological argument to support these ontogenetic differentiations.

Geometric morphometrics.—In order to complete the biometric study, geometric morphometric methods were performed on a set of landmarks defined from morphological points (Bookstein, 1991). The procedure allows comparing morphological patterns where each specimen has the same set of homologous landmarks. This method allows study of shape variation and its covariation with size (Bookstein, 1991).

The landmarks on cranidia and pygidia were obtained by the optic image analyzer tpsDig2 (Rohlf, 2006). The x- and

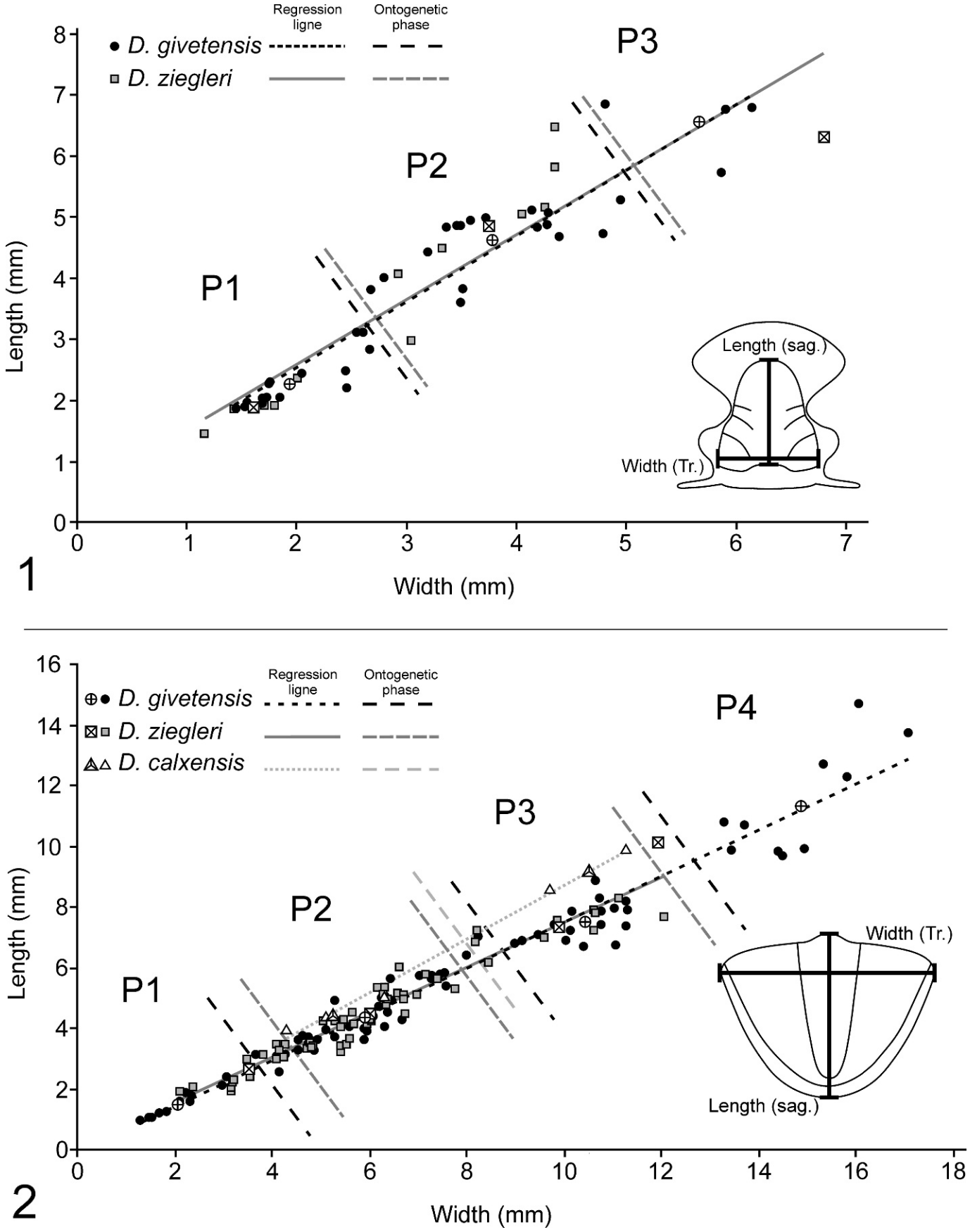

FIGURE 1—Scatter plot of width versus length: *1*, glabella without occipital ring; *2*, pygidia of *Dechenella givetensis* Bignon and Crônier, 2011, *D. ziegleri* Struve, 1992 and *D. calxensis* Bignon and Crônier, 2011. Cross represents the mean specimen for each ontogenetic phase. Three size groups labeled from P1 to P3 are proposed for cranidia and four labeled P1 to P4 for pygidia according to a hierarchical classification based on width and length linear dimension on each species (modified from Bignon and Crônier, 2011).

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TABLE 1—Statistical results of ANOVAs testing the differences among ontogenetic phases on the width and length of 39 glabellae without occipital ring and 137 cranidia, and the first two significant axes of the relative warp analysis of 17 cranidia and 42 pygidia.

Dechenella species		df	SC	MC	F	P
D. givetensis	Glabella length (sag.) without occipital ring	2	78.5437	39.2719	175.7	<0,0001***
	Glabella width (tr.)	2	55.4716	27.7358	88.89	<0,0001***
D. ziegleri	Glabella length (sag.) without occipital ring	1	25.5645	25.5645	30.6	<0,001***
	Glabella width (tr.)	1	13.3073	13.3073	46.87	<0,0001***
D. givetensis	Pygidial length (sag.)	3	652.6	217.533	196.9	<0,0001***
	Pygidial width (tr.)	3	1138.546	379.512	353.5	<0,0001***
D. ziegleri	Pygidial length (sag.)	2	129.374	64.6871	126.1	<0,0001***
	Pygidial width (tr.)	2	242.123	121.4563	156.8	<0,0001***
D. soetenica	Pygidial length (sag.)	1	27.4563	27.4563	58.27	<0,01**
	Pygidial width (tr.)	1	33.075	33.075	29.91	<0,05*
Cranidial shape (RW1)		3	0.0107	0.0036	7.014	<0,01**
Cranidial shape (RW2)		3	0.0050	0.0017	2.824	NS
Pygidial shape (RW1)		6	0.4889	0.0081	16.81	<0,0001***
Pygidial shape (RW2)		6	0.0033	0.0006	1.676	NS

y-coordinates of respectively eight and five landmarks were automatically extracted on 17 cranidia and 42 pygidia. Only 2-D projections of the dorsal views have been considered here (Fig. 2).

In order to estimate the landmark measurements error, five replicates were performed respectively on the same cranidium and pygidium. ANOVAs applied on each coordinate of landmarks indicate no significant (NS) morphological differentiation among replicates ($P > 0.05$, NS). Some individuals are slightly deformed tectonically by a single direction of stretching. Flattening does not seem to occur. Following Crônier et al. (2005) we used the retrodeformation method of Motani (1997) to integrate these distorted specimens in the morphometrical analysis. The x-axis is defined as the transversal direction and the y-axis as the sagittal one (Fig. 2). Firstly, a rotation adjusts the transversal direction of the specimens with the x-axis. Then a displacement gradient matrix makes the sagittal direction perpendicular to the transversal one. For further details see Crônier et al. (2005). Thirteen of 17 selected cephalic sclerites in the morphometrics analysis were retrodeformed (9/12 for *D. givetensis* and 4/5 for *D. ziegleri*) and 13 of 42 selected pygidial sclerites (9/29 for *D. givetensis*, 3/9 for *D. ziegleri* and 1/4 for *D. calxensis*). The retrodeformed specimens are distributed between different species and ontogenetic phases, which provides a check to ensure that retrodeformation does not affect the reconstructed ontogenetic trajectory. For example, the sample size for the second ontogenetic phase in *D. givetensis* includes 12 undeformed and three retrodeformed pygidia. The angles between ontogenetic vectors of each group and the within-group variance were calculated by 400 bootstrap sets for each group at 95% confidence limits. Intra-group variance angles are greater (129.1° for unretrodeformed specimens and 45.0° for retrodeformed specimens) than the inter-group variance (34.5°). This result signifies that the variation within groups is greater than between them, so both ontogenetic trajectories are not significantly different. Consequently, retrodeformed specimens do not bias ontogenetic trajectories.

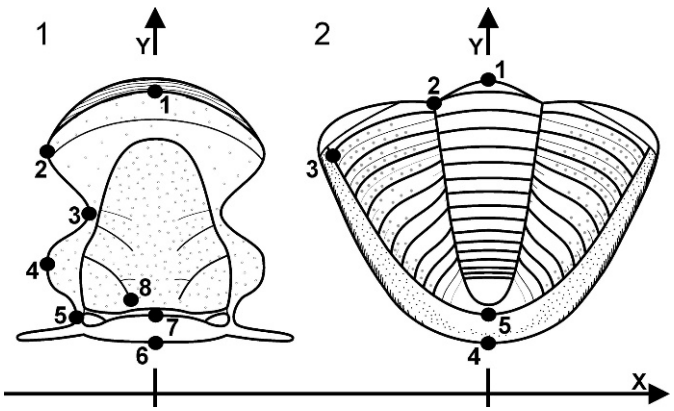

FIGURE 2—Landmarks selected for morphometric analyses of the ontogeny of three *Dechenella* species. Landmarks are captured on dorsal view and defined as follows for cranidium (1): *1*, anteriormost point of cephalon on sagittal axis; *2*, lateral extreme point of anterior section of facial suture (β); *3*, flexure point between anterior section of facial suture and anterior margin of palpebral lobe (γ); *4*, lateral extreme point of palpebral lobe (δ); *5*, flexure point between posterior margin of palpebral lobe and posterior section of facial suture (η); *6*, posterior midpoint of occipital ring; *7*, posterior midpoint of glabella; *8*, proximal tip of S1; and for pygidium (2): *1*, rachis anterior midpoint; *2*, anterior extremity of axial furrow; *3*, intersection of border furrow with first pleural furrow; *4*, posterior midpoint of posterior border; *5*, rachis posterior midpoint.

Superimposition methods eliminate size variations of the landmarks configurations by scaling and overlaying them according to some optimization criteria. Generalized Procrustes Analysis (GPA or Generalized Least Squares, GLS) superimposes landmark configurations using least-squares method for translation and rotation. Firstly, configurations are rescaled to a unit size and the centroid (squared root of the mean squared distance between the centroid and each landmarks; Bookstein, 1991) of each specimen is translated to the same origin in order to superpose them. Finally, configurations are rotated to minimize the squared differences between corresponding landmarks (Rohlf and Slice, 1990). The GLS superimposition was computed by the tpsSuper software v. 1.14 (Rohlf, 2004a).

Partial Warps refer to the components of the non-uniform deformation (Bookstein, 1991; Zelditch et al., 2004). Partial Warp Scores are the coefficients indicating the position of an individual relative to the reference along Partial Warps. Relative Warp Analysis (RWA; Rohlf, 1993) was performed to visualize the shape variation of ontogenetic phases for the cranidia (Fig. 3) and the pygidia (Fig. 4). This principal component analysis of the partial warp scores describes localized departures from the average configuration (Bookstein, 1991; Rohlf, 1993). The RWA defines new principal independent axes (Relative Warp, RW) according to a decreasing of the variance in the explanation of the shape variability. Significant RWs characterize a morphospace into which it is possible to locate each ontogenetic phase according to its coordinates on these RWs. ANOVAs applied on the matrix of scores on the RWs indicated a significant morphological differentiation among ontogenetic phases according to RW1 (Table 1). RWA is computed by the tpsRelw program (Rohlf, 2007).

The interpretation of morphological differences for cephala and pygidia is indicated by the ontogenetic vectors attached to

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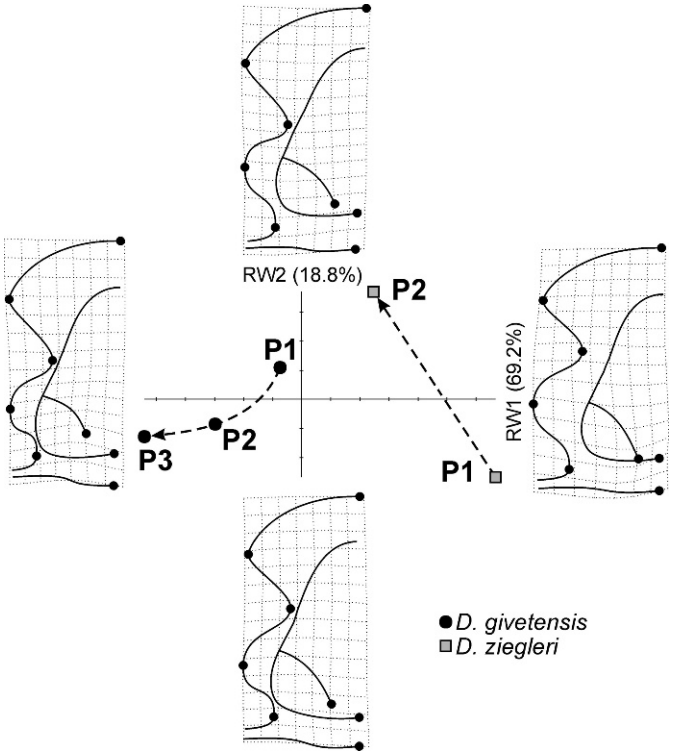

FIGURE 3—Location of the mean ontogenetic phases, labeled from P1 to P3, of *Dechenella givetensis* Bignon and Crônier, 2011 (circle) and *D. ziegleri* Struve, 1992 (square) cranidia in the morphospace defined by the first two relative warp RW1 and RW2 representing respectively 69.2% and 18.8% of the total variance. Thin-plate spline deformation grids depicting patterns of shape changes on each extremity axes.

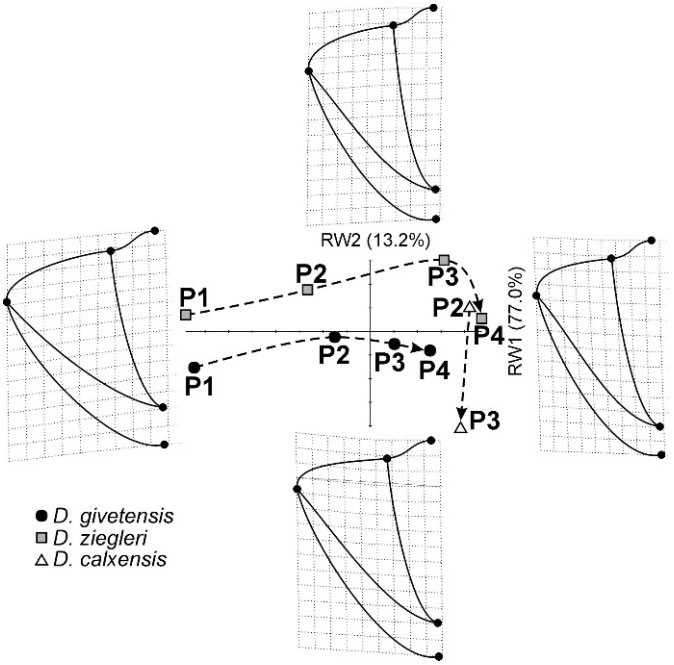

FIGURE 4—Location of the mean ontogenetic phases, labeled from P1 to P4, of *Dechenella givetensis* Bignon and Crônier, 2011 (circle), *D. ziegleri* Struve, 1992 (square) and *D. calxensis* Bignon and Crônier, 2011 (triangle) pygidia in the morphospace defined by the first two relative warp RW1 and RW2 representing respectively 77.0% and 13.2% of the total variance. Thin-plate spline deformation grids depicting patterns of shape changes on each extremity axes.

each landmark (Figs. 5, 6), showing the direction of maximum variance. Vectors were calculated using the GPA superimposition method (explained above) by the tpsSplin program (Rohlf, 2004b). These procedures were firstly performed between consensus of each species in order to quantitatively characterize their shape; secondly, between consensus of two successive ontogenetic phase (phases 1 to 2, phases 2 to 3, phases 3 to 4) in order to provide a visualization of the shape changes and amplitudes of each species.

The angles between ontogenetic vectors were calculated in order to compare the cranidial and the pygidial growth patterns of the different species (Fig. 7). Ontogenetic vector summarizes the magnitude and the orientation of shape modifications (with x and y components) of a landmark during ontogeny. The growth vector is computed from the linear regression of x and y component of ontogenetic vector of each landmark on the log centroid size. If the angle of growth vector variation within each species were greater than the angle of the variation between these two species, the ontogenetic patterns would be similar. Conversely, if the angle of the variation between two species were greater than the angle of growth vector variation within each species, the two ontogenetic patterns would be different (Webster et al., 2001; Zelditch et al., 2003a; Hunda and Hughes, 2007). Within-species variance was calculated by 400 bootstrap sets for each species at 95% confidence limits. The angle of the variation between ontogenies of the two species is significant if it exceeds the bootstrapped within-group variance at 95% confidence (see Webster et al., 2001 for further explanation on the procedure). The growth pattern was compared with VecCompar6c software in the Integrated Morphometrics Programs (IMP) package, compiled by H. D. Sheets and freely available electronically at http://www.canisius.edu/sheets/morphsoft.html.

For pygidia of *D. givetensis* and *D. ziegleri,* the partial Procrustes distance (Bookstein, 1991; Zelditch et al., 2004; Webster, 2007; Delabroye and Crônier, 2008) for each specimen and for each mean ontogenetic phase was plotted against the log centroid size (Fig. 8) in order to visualize the amount of shape differences during the ontogenetic development. The shape reference of each species corresponds to its smaller specimen. The partial Procrustes distance was computed by Regress6N software in the IMP package of Sheets (mentioned above).

RESULTS

Cranidia.—The cranidia of *D. givetensis* and *D. ziegleri* are well differentiated in morphological space corresponding to the first two relative warps representing 78% of the total variance (Fig. 3). Vectors of the mean specimen of each species were compared (Fig. 5.1). *Dechenella ziegleri* has a wider (tr.) and longer (sag.) palpebral lobe, a proximal tip of S1 more posterior, a slightly thinner (sag.) occipital ring and a shorter glabella-anterior border compared to *D. givetensis*.

The cranidial ontogenetic trajectories of *D. givetensis* and *D. ziegleri* in the morphological space seem opposite according to the second relative warps (Fig. 3). The ontogenetic modifications of *D. ziegleri* between phases 1 and 2 are greater than those of *D. givetensis* (Fig. 3). The main shape changes that took place during the ontogeny of *D. givetensis* are: 1) a proximal displacement of γ; 2) a palpebral lobe migrating posteriorly; 3) a forward (interphase *1–2*) and then a proximal displacement (phases 2 to 3) of η; 4) a narrowing of occipital ring (sag.); 5) a forward displacement of proximal tip of S1; and 6) an extension (sag.) of the cranidia (Fig. 5.2, 5.3). The

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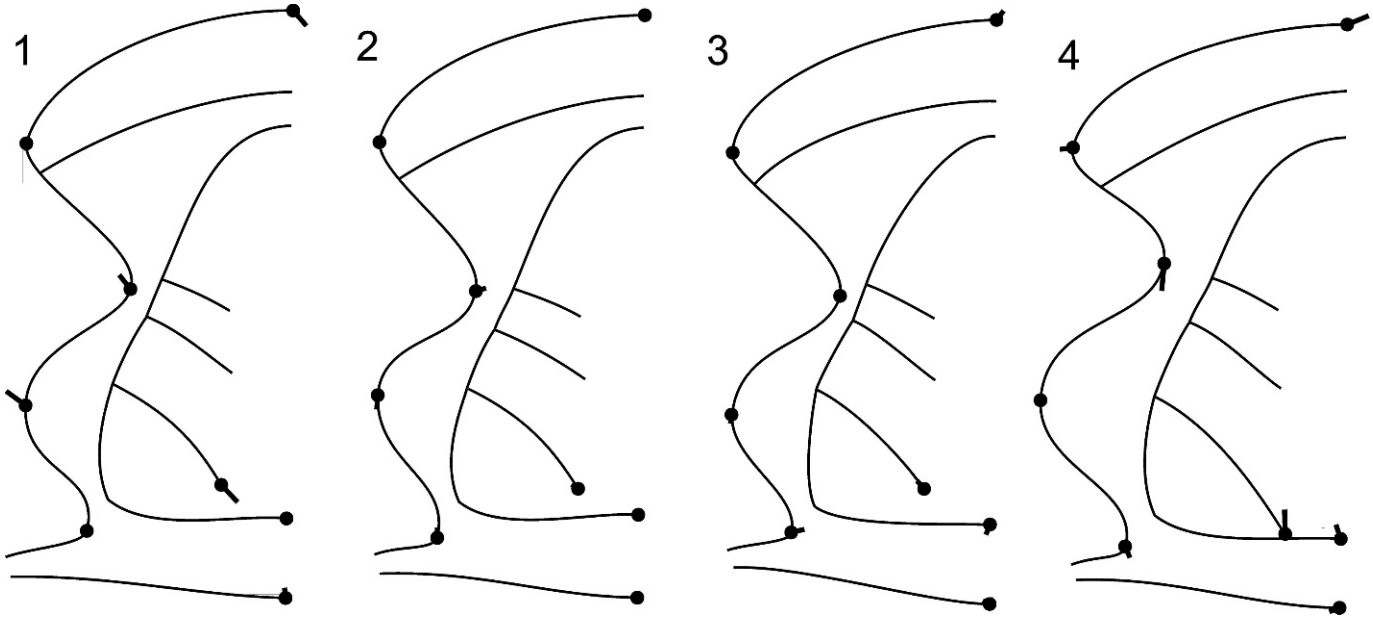

FIGURE 5—Vectors attached to each landmark indicating the direction of maximum variance of cranidia between: *1*, mean specimen of *Dechenella givetensis* Bignon and Crônier, 2011 (dots) and *D. ziegleri* Struve, 1992 (vectors); *2,* phases 1 and 2 (P1–P2) of *D. givetensis*; *3*, phases 2 and 3 (P2–P3) of *D. givetensis*; *4*, phases 1 and 2 (P1–P2) of *D. ziegleri.*

main shape changes that took place during the ontogeny of *D. ziegleri* are: 1) a widening of the anterior border (tr.); 2) a posterior displacement of γ; 3) a posterior displacement of η; 4) a widening (sag.) of occipital ring and 5) a forward displacement of proximal tip of S1 (Fig. 5.4).

Moreover the comparison of the intra- and inter-specific angles variation of the ontogenetic vectors confirms the differences in the cranidial ontogenetic trajectories of *D. givetensis* and *D. ziegleri* (Fig. 7.1). Only the ontogenetic phases 1 and 2 were tested because there was no specimen of *D. ziegleri* available for the third phase.

Pygidia.—The pygidia of *D. givetensis* and *D. ziegleri* are rather similarly distributed in the morphospace corresponding to the first two relative warps representing 90.2% of the total variance (Fig. 4). According to the vectors attached to the landmarks of the mean specimen of each species, *D. givetensis* differs from *D. ziegleri* only from a very slightly narrower (tr.) pleural field (Fig. 6.1).

The pygidial ontogenetic trajectories of *D. givetensis* and *D. ziegleri* are roughly parallel and mainly ordered on the first relative warp (Fig. 4). The main ontogenetic modifications for both species are: 1) a decrease of the pleural field width (tr.); 2) an elongation of the axis (sag.); 3) a thinner posterior border (sag.); and 4) a widening (tr.) of the axis (Fig. 6.3–6.5, 6.8–6.10). Moreover, most of shape changes occur before the second ontogenetic phase for *D. givetensis* (Fig. 6.3); the vectors were strongly reduced after this phase (Fig. 6.4, 6.5). The amplitude of the vectors for *D. ziegleri* is rather constant between the ontogenetic phases 1–3 (Fig. 6.8, 6.9).

Moreover, the comparison of the intra- and inter-specific angle variation of the ontogenetic vectors between *D. givetensis* and *D. ziegleri* confirms that the greater angle is intra-specific. The pygidial ontogenetic changes are more variable within each species than between both two species. Consequently the pygidial ontogenetic trajectories of these species could not be considered different (Fig. 7.2).

The bivariate diagram of the procrustes distance against log centroid size shows a growth model best fitted by a linear model for *D. givetensis* ($y=0.047x + 0.02$; $r=0.928$; $P< 0.001$***) and for *D. ziegleri* ($y=0.091x–0.05$; $r=0.956$; $P< 0.001$***; Fig. 8). Although ontogenetic vectors are not different (Fig. 7.2), the comparison of these two linear trajectories shows that the linear trajectory of *D. ziegleri* is more sloped than the ones of *D. givetensis*. Additionally, in comparing these two independent samples, an F-test (Brandt, 1983) provided a measure of the probability that both trajectories have the same variance or regression model (Lomax, 2007). Thus, a significant difference between the two ontogenetic trajectories was detected on the slopes ($P< 0.001$***). This significant difference on the slope suggests that the shape modifications during ontogeny are stronger for *D. ziegleri* than *D. givetensis* at least in the studied interval.

The ontogenetic phases of *D. calxensis* have a marginal position in the morphological space compared to the two other species (Fig. 4). This marginal position corresponds to: 1) a smaller pleural field width (tr.); 2) a narrower axis (tr.); 3) a longer (sag.) rachis; and 4) a thinner posterior border (Fig. 6.2, 6.6). Nevertheless, *D. calxensis* has a more curved (more elevated) pygidium in posterior view, which results in a smaller (tr.) axis and pleural field in dorsal view.

Additionally, the pygidial trajectory of *D. calxensis* is different of *D. givetensis* and *D. ziegleri* ones (Fig. 4). Indeed, the ontogenetic trajectory shows only variations on the second relative warp. The shape changes between the ontogenetic phases 2 and 3 correspond to: 1) a more transversal anterior border of the pleural field; and 2) a widening (tr.) of the axis (Fig. 6.7).

Comparison between the intra- and inter-specific angle variations of the ontogenetic vectors confirmed the differences between the pygidial ontogenetic trajectories of *D. calxensis* and *D. givetensis* (Fig. 7.3) one the one hand, and of *D. calxensis* and *D. ziegleri* (Fig. 7.4) on the other hand. Only ontogenetic phases two and three were tested because there was no *D. calxensis* specimen available for the first and fourth phases.

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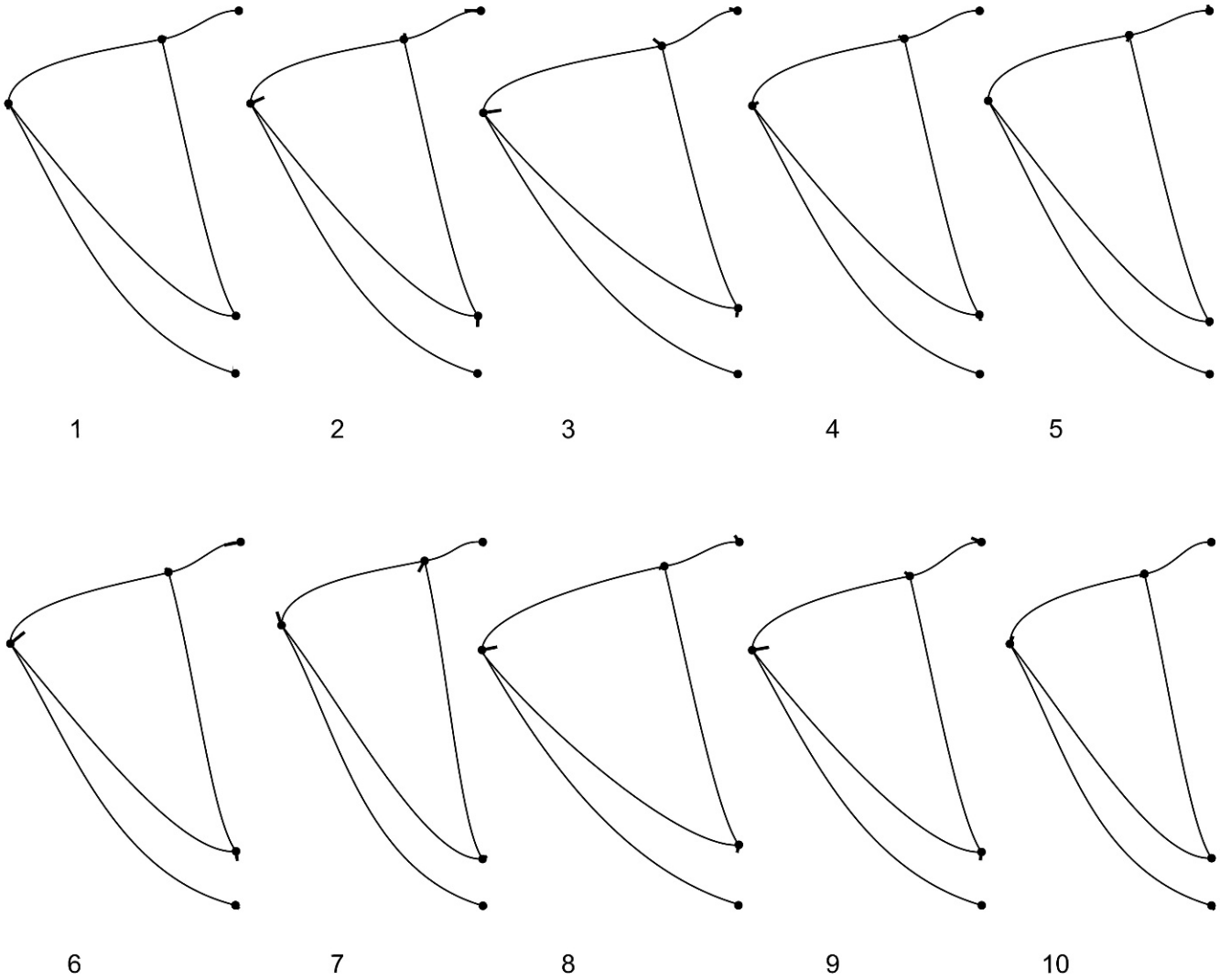

FIGURE 6—Vectors attached to each landmark indicating the direction of maximum variance of pygidia between: *1*, mean specimen of *Dechenella givetensis* Bignon and Crônier, 2011 (dots) and *Dechenella ziegleri* Struve, 1992 (vectors); *2*, mean specimen of *D. givetensis* and *Dechenella calxensis* Bignon and Crônier, 2011; *3*, phases 1 and 2 (P1–P2) of *D. givetensis*; *4*, phases 2 and 3 (P2–P3) of *D. givetensis*; *5*, phases 3 and 4 (P3–P4) of *D. givetensis*; *6*, mean specimen of *D. ziegleri* and *D. calxensis*; *7*, phases 2 and 3 (P2–P3) of *D. calxensis*; *8*, phases 1 and 2 (P1–P2) of *D. ziegleri*; *9*, phases 2 and 3 (P2–P3) of *D. ziegleri*; *10*, phases 3 and 4 (P3–P4) of *D. ziegleri*.

DISCUSSION

Morphometric and statistic analyses on cranidia of *D. givetensis* and *D. ziegleri* demonstrate a clear difference in their ontogenetic trajectories. Such developmental modification corresponds to an allometric repatterning (sensu Webster and Zelditch, 2005). Since the allometric patterning is not conserved, these differences could not be treated as a heterochronic event, which concerns only a modification of 1) change speeds; 2) development duration; or 3) succession of developmental events. The observed differences in growth patterns correspond to a length reduction (sag.) of the facial suture posterior section and of the fixigenal field (tr.) between γ and the glabella for *D. givetensis* whereas these differences correspond to an increase of the occipital ring width (sag.) and anterior border (tr.) length and a posteriorly move of γ and η for *D. ziegleri*.

The quantitative analysis show weak shape changes of cranidia for *D. givetensis* and *D. ziegleri*. Lerosey-Aubril and Feist (2006) have demonstrated that several Proetoidea taxa seem to change their feeding habits during the meraspid-holaspid period (even within holaspid period) passing from predatory/scavenger to particle feeder and vice-versa. These changes imply important modifications of the cephalon such as appearance/disappearance of a plectrum and contact or not between glabella and anterior border furrow. *Dechenella givetensis* and *D. ziegleri* do not show such modifications during their cranidial ontogenetic development and could have retained the same diet during developmental periods considered on this study. However it cannot be possible to exclude another feeding habit for the youngest specimens that are not included in this analysis.

There is no significant difference between the ontogenetic vectors of *D. givetensis* and *D. ziegleri* for pygidia. This similitude implies that these species share the same pattern of shape changes during the development (Fig. 7.2). However, their rate of ontogenetic modifications is different (Fig. 8). Consequently, a rate modification (Webster and Zelditch, 2005) is the best fitting mode of ontogenetic modifications to consider this pattern. A rate modification is often coupled with an allometric repatterning (Hughes and Chapman, 1995; Zelditch et al., 2000; 2003b) but not in this case. Compared to

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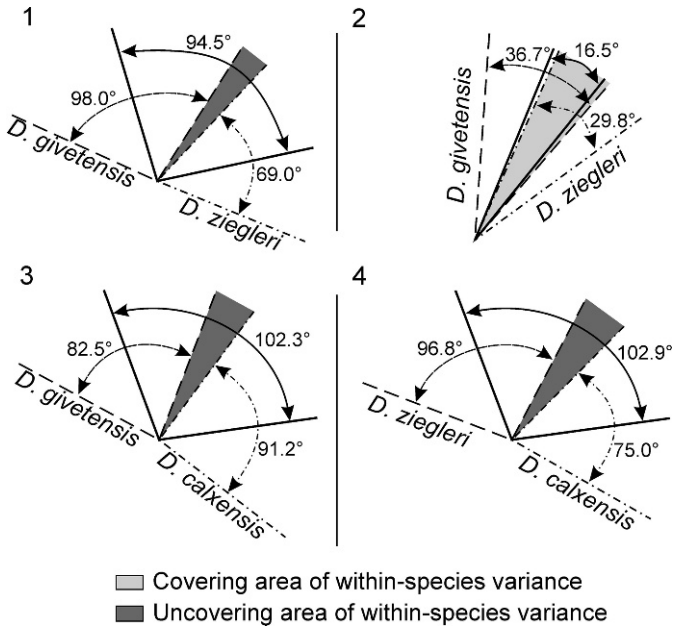

FIGURE 7—Within and between-species comparison of pattern of shape changes during development. Comparison based on vectors calculated using Bookstein registration. Within angles calculated from 400 bootstraps given at 95% confidence limits. Between-species considered statistically significant if the angle between ontogenies exceeds within-species angles at 95% limits. Between-species angle exceed within species angles of ontogenetic trajectories for *1–4*: *1*, cranidia of *Dechenella givetensis* Bignon and Crônier, 2011 and *Dechenella ziegleri* Struve, 1992; *3*, pygidia of *D. givetensis* and *Dechenella calxensis* Bignon and Crônier, 2011; *4*, pygidia of *D. ziegleri* and *D. calxensis*; *2*, between-species angle does not exceed within species angles of ontogenetic trajectories pygidia of *D. givetensis* and *D. ziegleri.*

D. givetensis, the stronger ontogenetic modification for *D. ziegleri* leads the older specimens to have a longer (sag.) pygidial axis, a thinner posterior border (sag.) and pleural field (tr.).

An additional noteworthy feature was the presence of a postero-medial notch on the pygidial border in the earliest ontogenetic stages of *D. givetensis* (Bignon and Crônier, 2011). This notch disappears rapidly and progressively before the beginning of the second ontogenetic phase. The same feature has been already reported in other *Dechenella* such as *D. neotesca* Ormiston, 1967, *D.* cf. *planimarginata* Ormiston, 1967 and other Devonian Proetidae as *Cyrtosymbole* Richter, 1913 (Feist and Lerosey-Aubril, 2005) and *Drevermannia* Richter, 1913 (Lerosey-Aubril, 2006). This notch is absent in equivalent ontogenetic phases of *D. calxensis* and *D. ziegleri*. The presence/absence of the notch in the earlier stage represents a case of static mode of ontogenetic modifications corresponding to a heterotypy (sensu Webster and Zelditch, 2005). However, absence of the postero-medial notch in *D. ziegleri* and *D. calxensis* may result from an increase of notch loss rate. If this assumption is true, it can be predicted that younger specimens would have possessed such a notch. Therefore, only the discovery of such younger specimens of *D. ziegleri* and *D. calxensis* could change our interpretation from a heterotypy to a rate modification.

We decided not to specify the direction of evolutionary changes between these species. Indeed, definition of their 'ancestor-descendant' relationships is, in the present state of knowledge, too speculative. The last phylogeny of this genus was performed by Lieberman (1994), mostly on U.S. species. Since this paper, a lot of species were described in Europe, and Basse (2002) defined a new classification based on five groups of species without phylogenetical framework. These five groups do not correspond to Lieberman's (1994) clades. An update is necessary prior to make assumptions on the direction of evolutionary changes.

Nevertheless, these species could be easily placed in the groups defined by Basse (2002). *Dechenella givetensis* and *D. calxensis* belong to the "*D. verneuili*" group and *D. ziegleri* to the "*D. granulata*" one. Consequently, the two first species are probably closer than the third even if the pygidial ontogenetic trajectories of *D. givetensis* and *D. ziegleri* are not statistically different. This remark could be surprising because the pygidial ontogenetic trajectories of *D. givetensis* and *D. ziegleri* are not statistically different (Fig. 8.2). Without a reliable phylogeny of this genus, it is not possible to understand why there is such conservation of ontogenetic pattern between two distant species. This is another illustration of the complexity of ontogeny modifications in evolutionary processes.

The pygidial ontogenetic modifications are probably associated with hydrodynamic forces and/or predation. Indeed, locomotion in water implies for benthic organisms a compromise between 1) a specific effort to maintain contact with the substratum, dislodgement strongly reducing survival; and 2) a high mobility leading to lower predation susceptibility (Martinez, 2001; Lau and Martinez, 2003). Large pygidial pleurae and posterior border probably increased the hydrodynamic pressure on the pygidium. Thus, important contact with the ground would increase trilobite mobility and their capacity to grip the substrate. Lau and Martinez (2003) have demonstrated with modern crabs that smaller specimens have more restricted mobility on a rugose substrate than larger and heavier individuals. This was probably also the case with trilobites. This might suggest that the development of hydrodynamic attributes that allowed better control over contact with the substrate was more important for juveniles. A change in the resource allocation during ontogeny seems to have led to an increase of the axis width (tr.) versus pleural width (tr.) ratio. The resulting stronger pygidium may have provided more resistance against predator jaw pressure. This assumption is supported by pygidial ontogenetic modifications of *D. givetensis* and *D. ziegleri* such as: 1) a gradual reduction of pleural width (tr.); 2) a widening (tr.) of the rachis ; and 3) a narrowing (sag.) of the posterior border .

No global pattern could explain the ontogenetic evolution of *D. givetensis* and *D. ziegleri*. This study constitutes an additional illustration of mosaic evolution. Indeed, an allometric repatterning is recognized for cranidia whereas a rate modification in the latest stage and a heterotypy/rate modification in earlier stage are recognized for pygidia. A pattern of local heterochronies (Fink, 1982; McKinney, 1984; Edgecombe and Chatterton, 1987) could be consistent with an allometric repatterning mode of ontogenetic modifications. Nevertheless we cannot reject the assumption that the rate modification has a global effect on the organism. Indeed the allometric repatterning identified for cephala could disturb the signal of the rate modification if such pattern exists, thus preventing its recognition.

CONCLUSION

Our analysis characterizes, via geometric morphometrics, the cranidial and pygidial morphology of three *Dechenella* species and provides the first quantitative developmental description for this genus. Our analysis reveals a complex pattern of modes of evolutionary modifications of ontogeny. Significant differences in the development of cranidia for *D.*

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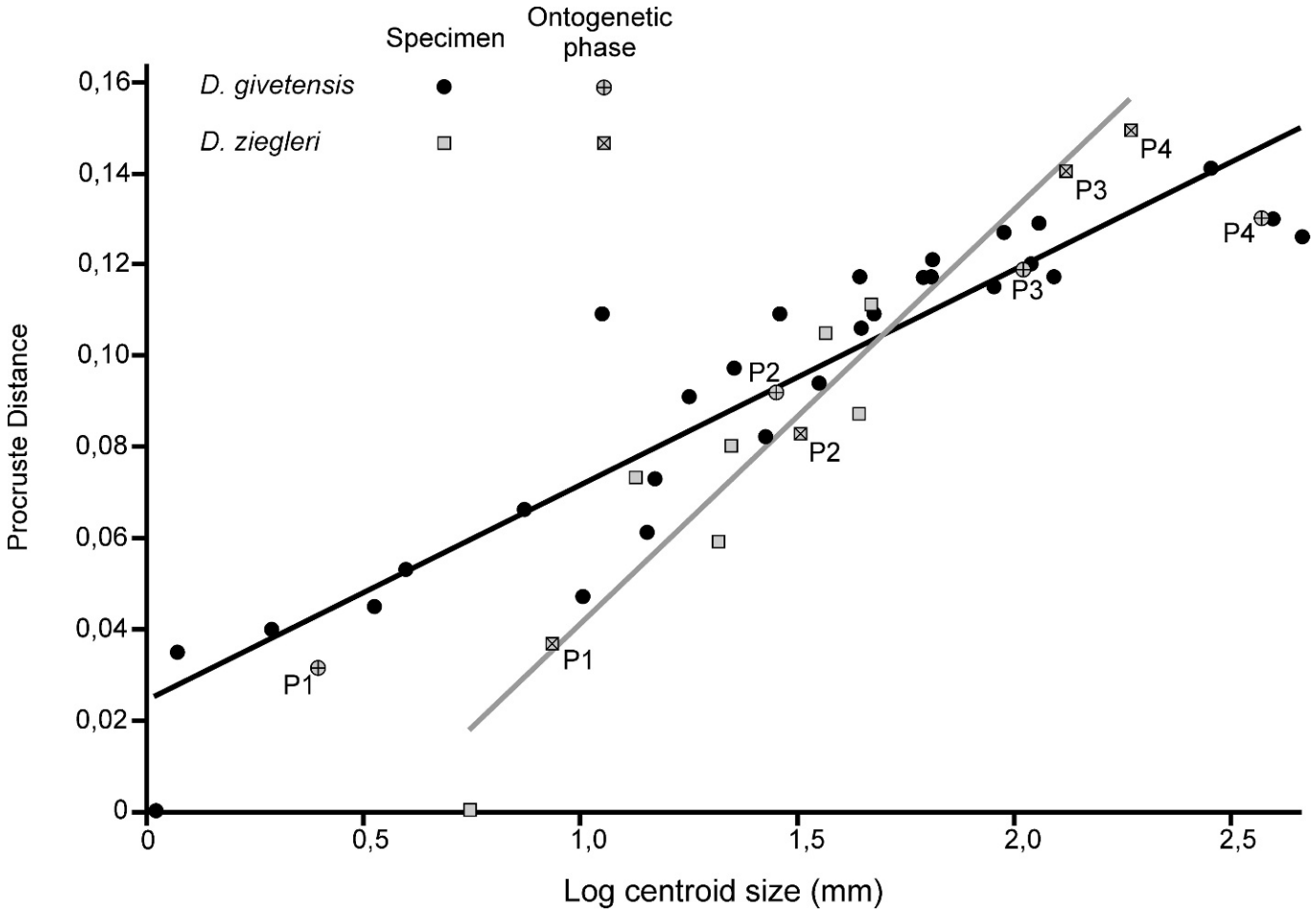

FIGURE 8—Relationship between size and shape of pygidia during the ontogeny of *Dechenella givetensis* Bignon and Crônier, 2011 (circle) and *D. ziegleri* Struve, 1992 (square). Shape is estimated by the procruste distance and the size by the centroid size. A regression lines has been fitted for each species having more than two described ontogenetic phases. Ontogenetic phase are labeled from P1 to P4.

givetensis and *D. ziegleri* correspond to an allometric repatterning. Only slight differences in the development of pygidia have been reported for these two species and correspond to a rate modification. The development of pygidia of *D. calxensis* is distinct from both other species where an allometric repatterning has been identified. Finally a heterotypy or a rate modification has been identified for the posterior-medial notch of pygidia.

These different ontogenetic patterns showed that the disparity was the result of a complex superimposition of several evolutionary modifications. The developmental reorganizations seem to be mostly located on a morphological structure in order to fit a particular environmental stress, as for example, the mode of nutrition for cranidia or the hydrodynamic conditions for pygidia.

Our analysis of *Dechenella* suggests the importance of ontogenetic modifications in the evolutionary processes in this plexus, and that these patterns could well have led to traits that were favorable for specific ontogenetic phases.

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